

Linking Phylogenetic Systematics to Evolutionary Biology: toward a Research Program in Biodiversity

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"Les recherches d'histoire naturelle, même celles qui ne semblent être que de pure et de vaine curiosité, peuvent avoir des utilités très réelles, qui suffiroient pour les justifier auprès de ceux mêmes qui voudroient qu'on ne cherchât que des choses utiles, si avant de les blâmer on avoit la patience d'attendre que le temps eut appris les usages qu'on en peut faire".

(DE RÉAUMUR, 1719)

As a matter of epilogue for a volume dealing with comparative studies, and although we hope that the reader is (now) convinced of the usefulness of phylogenetics, we would like to conclude in retrospection with the situation of systematics among life sciences.

This situation may be explained in the frame of evolutionary biology, because systematics deals with the study of organisms with regard to their natural relationships which are evolutionary patterns. Although self-evident, this matter of fact is often neglected. This oversight as well as some current received wisdoms concerning systematics must be exposed because they impede the realization of major syntheses and integrated studies in biological sciences.

Life sciences seem now on turn to be revolutionized by their two extremities. On one hand, biological processes are more and more thoroughly analyzed using molecular techniques and a single organism now includes virtually hundreds of wide research fields. On the other hand, we better and better understand how to compare and infer relationships between organisms using

modern phylogenetic methodology. Advances in these two extremities are the most recent manifestation of a long-lasting epistemological dichotomy, general biology versus comparative biology, "Investigations can seemingly inquire about either the uniformity of life or the diversity of life, aspects that can be referred to as general biology and comparative biology, respectively" (NELSON & PLATNICK, 1981).

Advances in general biology seem quite gradual at least with the continuous addition of new technical means and conceptual tools, and the discovery of new biological structures, from the organism to the cell, to the chromosome and to the gene and biomolecule. The increase of knowledge in this gradualistic perspective is indeed exponential.

Advances in comparative biology have been more punctuated with the recent and definitely new phylogenetics elaborated according to HENNIG's (1950, 1966) methodological principles, following former conceptions dating back at least to eighteenth century. These principles brought a total revolution in the definition of relationships, turning down both intuitive classifications and unproper similarity algorithms. Organisms may now be compared with a clear reference to their phylogenetic relationships – *i.e.* to their evolutionary history – and not only as different items vaguely placed in an intuitive or misleading classification.

The main challenge of the next decades will be to unify biology by the implementation of a research program aimed at connecting general and comparative biology (Fig. 1). It would not be sound to only analyze and understand more and more processes in a few unrelated organisms (*e.g.* *Drosophila*, *Rattus*, *Homo*, *Arabidopsis*, etc.), or to only produce tens of phylogenetic trees and classifications for little-known organisms (KELLOGG & SHAFFER, 1993). This challenge will probably suffer resistance from *a priori* anthropocentric and utilitarian-centered views which

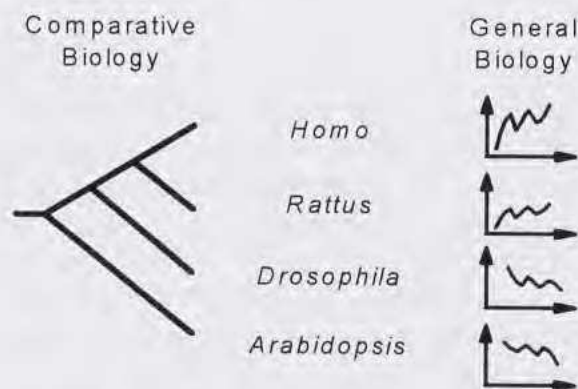


FIG. 1. — Connecting general and comparative biology in a same research program will make necessary to take into account that few model organisms are studied by general biology and that they should be combined in the frame of phylogenetic relationships to be fully interpretable in the light of comparative biology and evolution.

have always been very common in science and have tried to constrain its development in a way detrimental to *both* its usefulness and the increase in knowledge (*e.g.* DE RÉAUMUR, 1719).

The famous aphorism "nothing makes sense in biology, except in the light of Evolution" (DOBZHANSKY, 1973) is highly significant in this respect. We may paraphrase: nothing makes sense in biology, except in the light of a phylogenetic system which permit to consider all

processes in a complete historical perspective. This is true indeed for all studies in biology, even if some researchers often do not fully realize that their conclusions totally rely on the concept of phylogenetic relationships: for example, many hypotheses of evolutionary convergence are commonly accepted for two structures, two states or two processes without recognizing that these hypotheses can *only* be substantiated by a genuine phylogenetic reference – we mean they cannot be said substantiated by an old and intuitive classificatory scheme.

STUDYING EVOLUTION IN POPULATIONS OR EVOLUTION IN CLADES?

From the beginning, Evolution was perceived as a theory which needed to be substantiated not only according to the observation of patterns but also according to assumptions about processes at work (PERRIER, 1886). The promoters of the idea of evolution imagined processes such as spontaneous generation and inheritance of acquired characters (LAMARCK, 1809) or, later, descent with modification and natural selection (DARWIN, 1859) to explain the origin of hierarchical, inclusive and ordered patterns they observed.

The rise of genetics and ecology at the beginning of our century confirmed the existence of descent with modification and promoted natural selection as a major process in evolution. Evolutionary biology became a science of process and interest for tokogenesis replaced interest for phylogenesis (TASSY, 1991). Evidence for this fate is found in the assertion of some evolutionists who have argued that the great epoch of systematics or phylogeny, in terms of discovery, is the past, dating back to the eighteenth century, when the binominal nomenclature

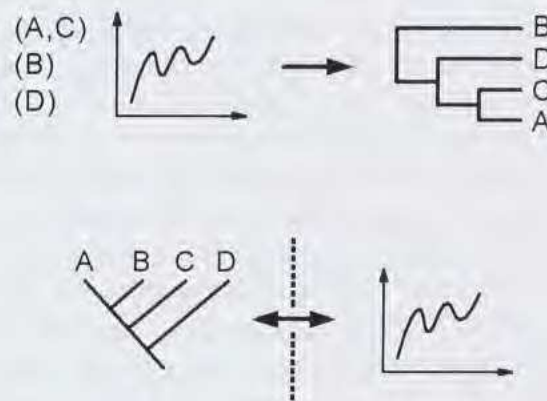


FIG. 2. — The first scheme above summarizes the former procedure of explanation in evolutionary biology (in an hypothetical group [A, B, C, D]): processes (e.g. selective regime, reaction norm, heritability) and traditional taxonomic levels were used to explain away patterns. The second scheme beneath summarizes the procedure of phylogenetic tests of evolutionary scenarios: both patterns in clades and processes in populations or organisms are actually studied, and the results are compared in a genuinely heuristic way.

and then the idea of evolution appeared (MAYR, 1982). The concept of natural selection, now central to present evolutionary biology, has put the patterns in the shadow (ELDRIDGE & CRACRAFT, 1980), although the main promoter of natural selection, Charles DARWIN himself, clearly acknowledged the important duality of pattern and process (DUPUIS, 1984, 1992).

In this context, evolutionists focused on processes which were either extrapolated to explain patterns in *ad hoc* narrations as nicely emphasized by ELDREDGE & CRACRAFT (1980), or were combined with patterns in a same *synthetic* – we mean artificial – and pleasant explanation of evolution (*e.g.* MAYR, 1963) (Fig. 2, above). From this point of view, many evolutionary studies were carried out on organisms and populations since the beginning of the century. These studies obviously focused on the processes existing within organisms and populations and extrapolated them back to the past macroevolutionary events. BROOKS & MCLENNAN (1991) concluded from a fair retrospective that an eclipse of true historical studies occurred in ecology and ethology because of lack of phylogenetic and comparative studies. Indeed, most historical studies were carried out by extrapolation and failed to analyze the past. This assertion does not concern paleontological studies which deal *per se* with the past and suffer from another kind of extrapolation, the hypotheses of actualism (NEL, 1997 in this volume).

Extrapolation of our knowledge to past and unknown phenomena is certainly an heuristic means to propose provocative hypotheses but it is not a fair way to validate these hypotheses. Extrapolation is in itself a model comprising not only factual knowledge but also many unwarranted hypotheses (mainly hypotheses by analogy from the present to the past). Thus, we need to study evolution both in clades and in populations. Evolutionary biology must not be restricted to the study of only one of these fields, on pain of either ignoring the diversity of processes and their respective roles, or being unable to generalize the role of well-known processes to explain the diversity of life in itself.

THE NATURE OF SYSTEMATICS AND SOME RECEIVED WISDOMS

Systematics is useful in evolutionary biology because it is central to studies of evolutionary patterns. But today it carries certainly an odd image in life sciences. After a great period of discovery and importance a hundred of years ago, it has been considered afterwards by many people as a marginal discipline in life sciences, a kind of narrative task whose goal is seen as to give unpronounceable latin names to as many species as possible, thus perceived by many researchers as “not modern science, not good science”. In this perspective, the systematist would be only bound to identify specimens provided by other scientists who need names, and some have added nowadays to the basic requirement – latin names –, a classification or a phylogenetic tree.

Let us abandon this incomplete image. In systematics as in any other science, data must be collected first (field sampling of organisms), they must be described and analyzed (description of taxa and phylogenetic inference), and interpreted (evolutionary histories drawn from phylogenetic trees). It is this whole set of activities which can be used to answer scientific questions concerning evolution. Systematics does not only provide people with names and classifications – which are obviously useful – but also with a reference system in evolution (phylogenetic trees). The reference system itself is not only a system for storing and retrieving information concerning names, but also a very powerful means to draw evolutionary histories for traits of interest (ELDREDGE & CRACRAFT, 1980).

Systematics – which was and which still is the science of evolutionary patterns – has been revitalized these last decades by methodological advances (HENNIG, 1950, 1966): it can now generate refutable assumptions about evolution, which can be freed from evolutionary models derived from population studies. Modern systematics is independent from these evolutionary models because it only uses the principle of descent with modification (the minimal concept of

Evolution) to explain patterns, *i.e.* “aspects of the apparent orderliness of life” (ELDREDGE & CRACRAFT, 1980: 1). At the opposite, population or organismic studies search for processes, “mechanisms that generate these patterns” (ELDREDGE & CRACRAFT, 1980: 1).

This is the opportunity to reconcile both approaches in the study of evolution. Patterns and processes must be studied in their respective domains – clades and populations – and be compared afterwards to derive better-corroborated hypotheses about the past (Fig. 2).

In this perspective, several received wisdoms may be found in the literature that obscure the actual role of systematics in today life sciences. These received wisdoms must be denounced to fully allow integrated studies of evolution to develop, using systematics and population biology.

Is there still something to search for at the taxonomic-organismic level?

Many speculations have been produced during these last years about the number of extant species. Whatever may be the number of unknown taxa, it is obvious that many remain to be found. A better question should be answered: do unknown taxa represent uninformative replica of already known taxa or original and “useful” new taxa?

Most research scientists know that it is impossible to simply answer such a question “yes” or “no”, because research is not a straightforward activity and wonderful results are often provided which differ from original conceptions or research fields.

A valuable answer to this question may be twofold. First, the frame of knowledge is not uniform: it is necessary to understand that past studies of biodiversity have not dealt randomly with faunas and floras for two or three centuries: some places or organisms were sampled over and over, some others were ignored. Important gaps in knowledge remain and must now be filled up, if one wants to have a good estimate of the contents of biosphere. Many scientific disciplines rely on such accurate estimates of these contents. Second, a prospective attempt may be done, using retrospectives of recent periods: many problems of biology have been solved thanks to an increase of knowledge of faunas and floras, for example when one taxon recently discovered gives up “the solution”. It can be a fungus responsible for a local resistance against a dangerous illness in trees. It can be an insect species corroborating a famous hypothesis concerning the evolutionary process of social behavior. For all these reasons, it is clearly necessary to search for new taxa in faunas and floras.

However, these taxa must be searched for through modern and integrated field and laboratory studies by experts in a scientific discipline and in a group of organisms (recording ethological, ecological, biochemical, etc. information), and not essentially searched for in blind mass-collecting as practiced during the last centuries or even still recently. It is only in this way that scientific research can take rapidly benefit from systematics, also because the information relevant to the question the investigator wants to answer is sampled together with the specimen (CODDINGTON *et al.*, 1991).

Morpho-anatomy versus molecules?

New research fields opened out during these last decades in relation to outstanding technical advances in molecular biology. Consequently, enthusiastic professions of faith appeared which predicted revolutions in the understanding of Evolution. Newly available tools appeared especially powerful to people who simply forget that there already exist tools positively useful to

reconstruct phylogenies and that already allow most available and robust phylogenetic hypotheses to exist (morphology, anatomy, histology, etc.), as shown by the retrospective of SANDERSON *et al.* (1993). For example, for the period 1989-1991, more than 40% of published phylogenies in high-standard journals were based on morphology.

It is still very common to read such kind of unfounded assertions: “A second reason for the surge of interest in comparative studies is that phylogenetic relationships among extant organisms are being estimated with increasing precision, largely as a result of advances in molecular biology” (HARVEY *et al.*, 1996) or “During the last decade, [...]. Together with improved phylogenies based on, for example, molecular sequence data, DNA hybridization, and other molecular methods [...], it will lead to a dramatic increase in the power of comparative studies for clarifying selection and evolution.” (ANDERSSON, 1994). This plea is however true for the organisms which are by themselves structurally closer to molecules than to multicellular organisms (viruses, ...).

As emphasized by WÄGELE & WETZEL (1994) or PHILIPPE (1997), molecular data cannot be the “only” or the “best” data which can be used to infer phylogenies, *because these qualifiers do not make sense a priori in science* (NELSON, 1994). Assertions of *a priori* explanatory contribution of any data set are misleading. For example, STEARNS (1992) asserted “Two key advances were HENNIG's (1950) introduction of phylogenetic systematics (also called cladistics) and molecular systematics, where the non-transcribed part of the genome provides data independent of the confusing changes that evolution can produce in phenotypes”. The dichotomy genotype/phenotype has nothing to do with phylogenetic methodology. For inferring phylogenies, *heritable* characters must be used whatever their very nature. How could we know *a priori* that evolution has produced more confusing changes in phenotypes than in genotypes in our case study? The value *a priori* of these characters is by definition unknown each time and cannot be extrapolated from one case study to another one.

In this perspective, molecular data are obviously very welcome to join the pool of other data – which needs to be as large and relevant as possible – and can help us in a number of cases to propose corroborated phylogenetic hypotheses (WENZEL, 1997 in this volume).

However, it is especially important not to throw out the baby with the bath water, and not to abandon morpho-anatomical studies and to shift completely toward molecular studies. *Both* studies are obviously necessary and complementary because we need to understand how both morpho-anatomy and genome evolved, because we need to combine reasonably independent sets of data and because we need the largest sample of data possible.

Are comparative studies too much speculative?

Many evolutionary biologists describe only the processes presently at work in populations. This may lead one to believe that only direct or experimental observations can be used to understand how evolution occurred because other observations such as comparative hypotheses – the phylogenetic patterns – may seem *a contrario* too circumstantial. In this context, *extrapolations* to the past evolution seem often correctly substantiated to many people, if they are based on such present observations.

The key-word in this point of view is “extrapolation”. The most careful studies of present-day processes must extrapolate to the past to generalize their results: we are unaware of one study of populational or organismic evolutionary biology which does not make assumptions to

extrapolate to past evolutionary events. This is indeed a most interesting and significant part of these studies, but the least substantiated.

As emphasized by one of us in the preface of this volume, these extrapolations are conjectural and may become either sound hypotheses or gratuitous speculation, depending on their refutability. Extrapolations can be refuted only if some independent patterns exist which allow to test them. This test is feasible using phylogenetic patterns, which do not depend on intentional assumptions of evolutionary processes. Phylogenetic patterns are the less gratuitous and the more refutable reconstructions of the past, because we only need for inferring them the basic hypothesis of descent with modification. Interaction between studies of present-day processes and studies of past patterns can provide us with well-corroborated results.

In conclusion, comparative hypotheses are not specifically speculative. Indeed, they prevent evolutionary hypotheses from being too much speculative.

Too many model organisms in too many studies?

To the eyes of practitioners of general biology, the plethora of taxonomic groups used by comparative biologists may be taken as an impossible scientific challenge and an unreasonable scattering of model organisms. This point of view is obviously related to an idiosyncratic perception of science by people who need to develop scientific studies in one model because of substantial technical feasibility constraints (KELLOGG & SHAFFER, 1993). For example, developmental genetics deals with very few organisms (DEUTSCH, 1997 in this volume). Comparative biology has not to cope with these limitations. On the contrary, comparisons by *homology* and by *analogy* are the very nature of comparative biology (NELSON, 1970; LORENZ, 1974). It is thus essential to increase the number of sampled clades used in comparative biology to test the generality of evolutionary patterns as far as possible. But these models must be carefully chosen to answer the questions of interest. It is not the number but the *a priori* quality of these models which has to be controlled (GRANDCOLAS *et al.*, 1997 in this volume).

Is the time scale of evolution compatible with phylogenetics and the sampling of biodiversity?

Famous studies of processes in populations (*e.g.* DOBZHANSKY, 1970; WHITE, 1954) have tied down the idea that evolution is generally rapid, except for a few relict species. Thus, sampling the biodiversity may be seen as an impossible challenge also for this reason: what is the need for describing species less rapidly than they appear and disappear?

First, some biologists studying processes have themselves considered that species may be relatively long-lived; for example, DOBZHANSKY *et al.* (1977) cited estimates ranging between 50,000 years and 1,000,000 years. Actually, many paleontological works have shown that present-day taxa may be very ancient or that, more generally, species may be relatively long-lived (for example, in insects, BRUNDIN, 1988, MATILE, 1990, 1997 in this volume, or in mammals, JAEGER & HARTENBERGER, 1989). Specifically, paleontology and comparative biology can show that the preconceived idea of necessarily rapid evolution is not generally true: biogeographers and paleontologists have documented that the present faunas include both recent and ancient stocks, the most ancient dating back to the Cenozoic or even to the Mesozoic. This is another example of misconceptions related to the only care of studies in general biology.

Generalizations may thus be false either because they are based on too few independent case studies or because they are based on *a priori* and totally speculative ideas. For example,

particular models of evolution have been hypothesized under which some kinds of phylogenetic reconstructions are flawed (e.g. FELSENSTEIN, 1978; FRUMHOFF & REEVE, 1988), but these models of evolution are impossible to assess *a priori* right or wrong in a particular case, *i.e.* prior to any phylogenetic reconstruction (see for example CARPENTER, 1997, and GRANDCOLAS *et al.*, 1997, both in this volume). So their usefulness is nil.

Biodiversity: what's in a word?

The concept of Biodiversity has nowadays a central position among scientific and political debates and policies. There are many different claims for its restriction to an organismic versus a genetic or a molecular significance, or to process versus pattern viewpoint. In our mind, the origin, maintenance and loss of biodiversity will be respectively better-known or prevented thanks to a high "biodiversity" of research scientists and scientific approaches.

The "biodiversity" of approaches should respect the natural hierarchy of research fields. What could be the meaning of genetic or molecular approaches without any population or organismic approaches (BARBAULT, 1988) and what could be the meaning of all these approaches without any phylogenetic framework? We could add, without any appropriate and recently corroborated phylogenetic framework.

As argued by DUPUIS (1992), this framework is not only a database system in which taxa and processes are stored and may be retrieved. This last view has been popularized because it emphasizes the most immediate and technological utility of systematics: identification and classification. No more systematists, no more identifications or classifications! This could be the immediate prejudicial effect that disappearance of systematics could have (e.g. WILSON, 1971; S.A. 2000, 1994).

But the phylogenetic framework is also an explanatory system which permits to test the macroevolutionary extrapolation of present-day processes and an heuristic system which permits to propose new research directions (JANVIER, 1984; PACKER, 1997 in this volume). In this way, phylogenetic systematics is a federating discipline and framework which connects all parts of life sciences and generates a research program in biodiversity.

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